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Climate change, grazing, and collecting accelerate habitat contraction in an endangered primate

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ABSTRACT

Correlational models are widely used to predict changes in species' distribution, but generally have failed to address the comprehensive effects of anthropogenic activities, climate change, habitat connectivity and gene flow on wildlife sustainability. Here, we used integrated approaches (MAXENT model, circuit model and genetic analysis) to assess and predict the effects of climate change and anthropogenic activities on the distribution, habitat connectivity, and genetic diversity of an endangered primate, *Rhinopithecus bieti*, from 2000 to 2050. We created six scenarios: climatic factors only (scenario-a), anthropogenic activities only (scenario-b), climatic factors and anthropogenic activities (scenario-c), plus three additional scenarios that included climatic factors and anthropogenic activities but controlled for individual anthropogenic activities (scenario-d: grazing, scenario-e: collecting, and scenario-f: grazing and collecting). The results indicate that areas of suitable habitat for *R. bieti* are expected to decline by 8.0%–22.4% from 2000 to 2050, with the collection of local forest products and the grazing of domesticated cattle as the primary drivers of landscape fragmentation and range contraction. If these anthropogenic activities are strictly controlled, however, the area of suitable habitat is predicted to increase by10.4%–14.3%. We also found that habitats vulnerable to human disturbance were principally located in areas of low habitat connectivity resulting in limited migration opportunities and increased loss of genetic diversity among *R. bieti* living in these isolated subpopulations. Thus, we suggest that effective management policies to protect this species include prohibiting both livestock grazing and the collecting of forest products. Although our study focuses on a single primate species, the conservation modeling approaches we presented have wide applicability to a broad range of threatened mammalian and avian taxa that currently inhabit a limited geographic range and are affected by anthropogenic activities (e.g. collecting, grazing, hunting), loss of habitat connectivity, reduced genetic diversity, and the effects of climate change.

1. Introduction

Global climate change is a major threat to ecosystems health and biodiversity, and is likely to have a significantly negative effect on species' distributions, population structure, genetic diversity, and the likelihood of survival (Bellard et al., 2012; Parmesan and Yohe, 2003). As a consequence of recent changes in temperature and rainfall patterns, a broad range of organisms are reported to have shifted their geographical distribution (McCarty, 2001; Wuethrich, 2000) including displacement toward the poles or to higher elevation (Root et al., 2003; Walther et al., 2002). The ability of individuals to track and successfully respond to shifting climatic conditions is constrained by intrinsic species-specific life history traits related to adaptability, as well as anthropogenic barriers to dispersal and gene flow, including the

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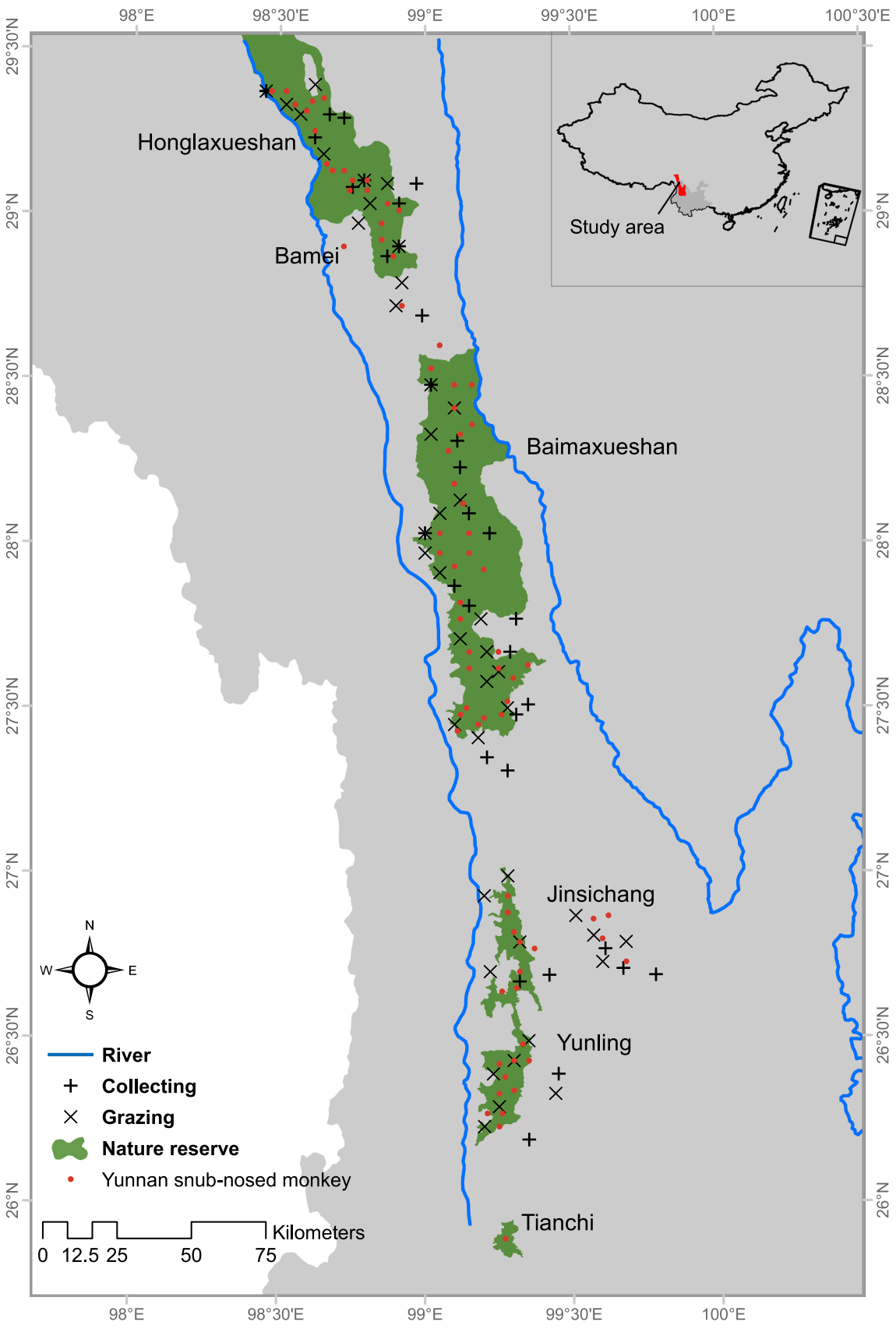

Fig. 1. The study site and locations of collecting and grazing areas.

construction of human settlements and roads, urbanization, and the conversion of natural ecosystems to agricultural fields and pastures (Kerr et al., 2015; Thomas et al., 2004; Estrada et al., 2017). In addition, Benítez-López et al. (2017) found that globally, hunting pressure in tropical forests was the highest in areas with greater accessibility, and that nearness to roads and settlements was among the most important factors contributing to hunting pressure in birds and mammals. Given that the negative consequences of anthropogenic activities are projected to increase significantly (Cleland et al., 2012; Salmona et al., 2017), modeling approaches designed to predict the future vulnerability of species under alternative change scenarios represent a critical tool for identifying effective pre-emptive conservation strategies (Polaina et al., 2016).

Globally, the joint effects of habitat loss and degradation resulting from anthropogenic disturbance and human-induced climate change represent a primary threat to the survivorship of the 27% of mammalian species that are currently listed as threatened with extinction (Schipper et al., 2008). In the case of China, 80% of 25 primate species are threatened, endangered or critically endangered (Li et al., 2018). Here we focus on the conservation status of the Yunnan snub-nosed monkey (*Rhinopithecus bieti*), a sexually dimorphic (adult male body mass ranges from15 to 40 kg, with adult males being twice as heavy as adult females) species of nonhuman primate endemic to China, that lives in social groups of several hundred individuals (Quan and Xie, 2002). A survey in the early 1990's indicated that this species was confined to a narrow region between the Yangtze and Mekong rivers (98°37′ to 99°41′E, 26°14′ to 29°20′N) with an estimated population size of < 2000 individuals (Long et al., 1994). The species' habitat is principally located in primary forest and is sensitive to anthropogenic activities including hunting, deforestation to create pastures for grazing, and the collecting of forest products (Long et al., 1994; Xiao et al., 2003). In addition, *R. bieti* avoid pastures and therefore habitat fragmentation functions as an effective barrier limiting dispersal and gene flow (Grueter et al., 2010; Kirkpatrick et al., 1998).

Based on evolutionary genetics and biogeographical data, the historical distribution and population genetic structure of snub-nosed monkeys appears to have been negatively impacted by environmental change and anthropogenic activities (Liu et al., 2009; Zhao et al., 2018). Over the past 2000 years, populations have been extirpated from central, southeastern and eastern China (Zhao et al., 2018). In the case of *R. bieti,* studies have shown that recent increases in temperature and rainfall may have served to expand habitat connectivity vertically and/or horizontally for some populations whereas for other populations, forest fragmentation is expected to increase and habitat quality to decrease, resulting in range contraction (Wong et al., 2013; Xiao et al., 2003). *R. bieti* are known to range to an altitude as high as 4500 m, which is the highest elevation reported for any nonhuman primate. Although this species original distribution is likely to have included both high and low elevation habitats (2500 m–4500 m above sea level), extant populations are restricted in their distribution to elevations of from 3000 to 4500 m. Global trends indicate that in response to recent increases in temperature, species have expanded its range to include higher elevation (Parmesan and Yohe, 2003; Root et al., 2003), and therefore we examined the degree to which suitable habitat for *R. bieti* may expand vertically in response to future changes in climate.

In the present study we systematically assessed and predicted the future effects of climate change and anthropogenic activities on the distribution and genetic diversity of *R. bieti* between the years 2000 to 2050. We hypothesize that if the rapid rate of land conversion that has occurred in China over the past 60 years continues, human activities will have the greatest impact on the future distribution of *R. bieti* and the greatest negative consequence for habitat connectivity and gene flow. Specifically we: 1) use several modeling approaches to predict the expected impact of climate change and anthropogenic activities on *R. bieti's* distribution, habitat connectivity, elevational change, level of gene flow, and genetic diversity under six impact scenarios; and 2) propose effective protection strategies for this species and for other endangered primates.

2. Materials and methods

2.1. Study area and data collection

This study was conducted across all current distribution areas of *R. bieti* in Yunnan and Tibet Provinces, China. Each of the wild groups was surveyed during the period from January to November 2013 and April to September 2016 and 2017. Because most wild groups are protected within nature reserves, we targeted our field investigation to all locations where this species is known to exist. We collected a total 92 GPS points in determining the location of *R. bieti* groups and deleted 17 GPS points within 1.5 km of a previously collected GPS point to avoid over estimating the number of existing social groups (published studies indicate that Yunnan snub-nosed travel an average distance of 1.5 km per day (Fig. 1; Kirkpatrick et al., 1998; Ren et al., 2008, 2009)). Thus, in order to test for spatial autocorrelation, we used the remaining 75 GPS points to calculate Global Moran's I (Moran's index = 0.081; Z = 1.38, $P < 0.05$).

In order to obtain accurate information on the effects of anthropogenic activities on *R. bieti* ranging behavior and patterns of habitat utilization, we conducted detailed surveys within the species main distribution across three national nature reserves (Bamaxueshan, Honglaxueshan and Tianchi), one provincial nature reserve (Yunling), and two sites outside of nature reserves (Jinsichang and Bamei) (Fig. 1). We investigated anthropogenic activities in the area surrounding *R. bieti* groups by recording the location of grazing areas (cattle) and local resource collecting areas using a GPS unit (Fig. 1). Detailed field surveys were carried out to obtain the precise locations of two disturbance-related variables: grazing (cattle) and collecting (collecting medicinal plants, fire wood, wild vegetables, and mushrooms). We sampled the spatial distribution of collecting and grazing areas at a resolution of 1 × 1 km.

Based on our long-term observations of *R. bieti*, we had previously determined that their alarm distance to the presence of humans is approximately 200–300 m, whereas their alarm distance to livestock is 100–150 m. This discrepancy in the monkeys' response to humans collecting forest products and to cattle grazing, was used to calculate the location and size of areas avoided (we scored 2 to collecting and 1 to grazing) and to construct an equal area projection that included both collecting and grazing layers (avoidance areas) in ArcGIS 10.2.2.

Estimates of factors that are likely to influence patterns of habitat utilization in *R. bieti* were derived using ArcGIS 10.2.2 and included distance to roads and distance to settlements. Road and settlement density were obtained from a 1:1,000,000 map of China (National Geomatics Center of China, data are available at http://atgcc.sbsm.gov.cn). Information on human population density, and location of pastures and areas of primary forest was extracted from HYDE3.2 (Goldewijk, 2016). Expected future (2015–2100 at 0.25 × 0.25 resolution) land use data (primary forest and pasture) were obtained from the World Climate Research Program Coupled Model Intercomparison Project (CMIP6). CMIP6 has developed the next generation of advanced Earth System Models (ESM), which are designed to estimate the combined effects of anthropogenic activities (e.g. land use and fossil fuel emissions) on the carbon-climate system (Hurtt et al., 2016). Data used to identify present and future land use scenarios as models' predictors come from http://luh.umd.edu/index.shtml.

In addition, nineteen bioclimatic variables at a 30 s resolution were obtained from the WorldClim database in order to represent climate information for 2000 (average for 1970–2000) as well as future climatic scenarios (average for 2041–2060) (available at http://www.worldclim.org). Climate data expected in the future were obtained from the BCC-CSM-1.1 global circulation model (GCMs), the IPCC-CMIP5 (the Intergovernmental Panel on Climate Change Fifth

Assessment Report), and from climate projections using the representative concentration pathway (RCP) 4.5. For the year 2050, the RCP4.5 predicts an average increase in global temperature of 0.9–2.0 °C. This represents a moderate effect of warming, in which carbon emissions peak around the year 2040 and decline thereafter, and this is expected to cause significant environmental changes in the future (Rehnus et al., 2018).

2.2. Analyses in MAXENT model

Using MAXENT modeling, it is critical to select variables that are specific to the ecology and behavior of the species studied and to only evaluate models based on their strength in predicting effects across a broad geographical area (Fourcade et al., 2018). We selected variables based on both the species' ecology and model fitting. We adopted the variable distance to settlements and distance to roads, as proxies for hunting pressures (Benítez-López et al., 2017). To calculate correlation coefficients between variables, we tested for collinearity among independent variables by removing one variable from each pair that was strongly correlated ($|r| > 0.8$; Cord et al., 2014). Several studies indicate that extremes in temperatures (costs of thermoregulation) and day length affect the ranging activities, activity budget, and timing of activities in *R. bieti* (Ren et al., 2009; Xiang et al., 2010; Grueter et al., 2013). Therefore, we accounted for this in our analysis using several climate variables. We then entered an environmental variables layer into the MAXENT model and selected the set of most important variables based on permutation importance, and reran the MAXENT models. Based on model fitting, we included the range in mean daytime temperature, isothermality, temperature seasonality, mean temperature of driest quarter, precipitation in driest month, and seasonality in precipitation in our analysis. Then we analyzed the correlation between non-climate variables and climate variables using "Raster Correlation and Summary Statistics" in ArcGIS 10.2.2 and deleted the variables with collinearity (Appendix 1-2).

To evaluate the cumulative impact of anthropogenic activities and climate change on *R. bieti* distributions, we created six scenarios: bioclimatic variables only (scenario-a), human disturbance variables only (scenario-b), bioclimatic variables and human disturbance variables together (scenario-c). Scenario-d, scenario-e and scenario-f included bioclimatic variables and human disturbance variables but controlled for anthropogenic activities (scenario-d controlled for grazing, scenario-e controlled for collecting and scenario-f controlled for both grazing and collecting) (Table.1). Because the construction of new roads and settlements are prohibited in the nature reserves, we used current variables (population density, distance to road and distance to settlement) in projections for 2050.

A MAXENT model was used to predict suitable habitat and altitude change for *R. bieti* in 2000 and in 2050. We randomly selected pseudo-absences and used 10,000 pseudo-absences with equal weighting for presences and absences, in order to yield the most reliable distribution models (Barbet-Massin et al., 2012).

Species occurrence data were divided into training sets (75%) for model building and testing sets (25%) for model evaluation, and then a subsampling procedure was conducted to evaluate the habitat suitability model by performing 10 replications in MAXENT (Khatchikian et al., 2011). Jackknife tests were used to estimate the importance of variables and the contribution of each variable to the model (Phillips et al., 2006). The performance measure is the area under the ROC curve (AUC), which measures the quality of the ranking of sites (Phillips et al., 2006). Models with values above 0.75 are considered to be potentially useful (Elith et al., 2011). Given that the MAXENT model estimates "relative" probabilities of species presence, we converted our results to presence and absence predictions based on the threshold values that maximized training sensitivity plus specificity (Liu et al., 2005). Cells falling above the threshold value were selected as suitable habitat for the species. The elevation data derived from the WorldClim database were used to calculate the mean elevation of potentially suitable habitat in ArcGIS 10.2.2.

2.3. Genetic analysis and circuit modeling

In order to assess the relationship between suitable habitat and genetic diversity, we conducted an analysis of gene flow among groups. The microsatellite and haplotype diversity data were obtained based on 135 individual *R. bieti* from 11 subpopulations from Liu et al. (2007, 2009). Gene flow among groups was estimated based on microsatellite data using MIGRATE 3.6.1 (Beerli and Felsenstein, 2001).

Circuit theory has strong application value in ecology, evolution, and conservation planning by bridging landscape and genetic data (McRae and Beier, 2007). Therefore we used Circuitscape 4.0 modeling software to treat landscapes as conductive surfaces and replacing cells to connect their neighbors with nodes linked by resistors (McRae and Shah, 2009). Electrical and genetic connectivity is similar to multiple or wide conductors that link two electrical nodes and allow for greater dispersal pathways than would a single, narrow conductor, with multiple or wider habitat swaths facilitating greater gene flow (McRae and Beier, 2007). In order to model and predict the potential dispersal pathways in different habitats, we used the habitat suitability maps produced by the MAXENT model as a resistance surface and constructed circuit models (Chetkiewicz and Boyce, 2009; McRae and Shah, 2009). We changed the range of conductance values from 0 to 1 because Circuitscape interprets zero conductance as a barrier. We estimated effective resistance between all possible pairs of cells to model habitat connectivity (Koen et al., 2012). We summed the current flow within each raster across the study area, thereby generating a continuous map that summarized movement probabilities between all source and target cells.

Table 1
Area of Suitable Habitat (km^2) for *R. bieti*.

Model	Variables		Time	AUC		Suitable habitat	Altitude (m)
	Bioclimatic	Anthropogenic activities		Training	Testing		
Scenario-a	Mdr, Iso, Ts, Mtdq, Pdm, Ps	–	Current	0.85	0.86	10,867	3738
			2050	0.86	0.88	9294	3847
Scenario-b	–	Gc, Pl, Pd, Pf, Dr., Ds	Current	0.85	0.91	5803	3649
			2050	0.85	0.92	5342	3641
Scenario-c	Mdr, Iso, Ts, Mtdq, Pdm, Ps	Gc, Pl, Pd, Pf, Dr., Ds	current	0.88	0.92	8294	3706
			2050	0.90	0.88	6434	3803
Scenario-d	Mdr, Iso, Ts, Mtdq, Pdm, Ps	G, Pl, Pd, Pf, Dr., Ds	2050	0.89	0.88	7102	3722
Scenario-e	Mdr, Iso, Ts, Mtdq, Pdm, Ps	Gc, Pl, Pd, Pf, Dr., Ds	2050	0.86	0.89	7197	3720
Scenario-f	Mdr, Iso, Ts, Mtdq, Pdm, Ps	Pl, Pd, Pf, Dr., Ds	2050	0.85	0.86	7356	3728

Note: Mdr: mean diurnal range; Iso: isothermality; Ts: represents temperature seasonality; Mtdq: mean temperature of driest quarter; Pdm: precipitation during driest month; Ps: precipitation seasonality, Gc: grazing-collecting; Pl: pastureland; Pd: population density; Pf: primary forest; Dr.: distance to roads; Ds: distance to settlements. Gr: Grazing, Co: collecting forest products.

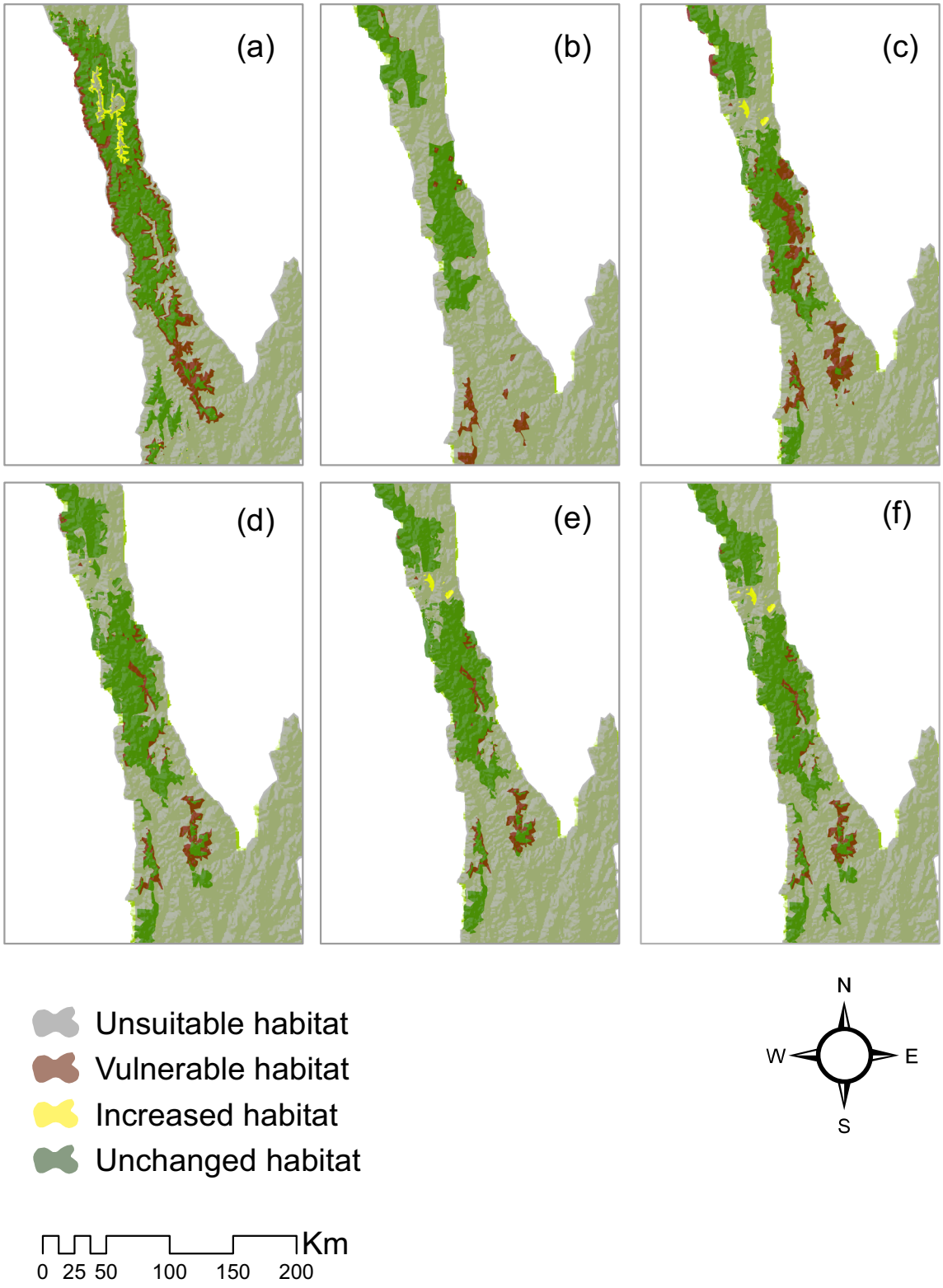

Fig. 2. Vulnerability analysis of the habitat available for *R. bieti* between the years 2000 and 2050 under six scenarios, (a) to (f). The data indicate changes across conditions between the years 2000 and 2050 under all scenarios Notes: Unchanged suitable habitat: the area in which suitable habitat remained largely unchanged under different scenarios; Vulnerable habitat: the area in which currently suitable habitat is expected to be converted into unsuitable habitat by 2050, or currently suitable habitat is expected to become unsuitable habitat in response to human disturbance; The generation of new areas of suitable habitat: the area in which unsuitable habitat is expected to become suitable habitat under different scenarios; and Unsuitable habitat: the area in which unsuitable habitat remained largely unchanged and unsuitable under different scenarios.

3. Results

The high training and testing AUC values produced by the MAXENT model under the six scenarios all indicated satisfactory performances (Table 1, Appendix 3). The results show that the area of suitable habitat for *R. bieti* was predicted to contract between the years 2000 to 2050 under three scenarios (reduced 14.5% under scenario-a, 8.0% under scenario-b and 22.4% under scenario-c, Table 1). In both 2000 and 2050, the availability of suitable habitat for *R. bieti* was the smallest under scenario-b, and collecting-grazing had an important effect on the monkey's distribution under scenario-b and scenario-c (Table 1 and Appendices 4–5). Compared with available habitat under scenario-c (2050), the area of suitable habitat in 2050 was predicted to increase by 10.4% in scenario-d, 11.9% in scenario-e and 14.5% in scenario-f. We found that areas of suitable habitat contracted in the Yunling Nature Reserves and at the site of Jinshichang (Fig. 2). In addition, the mean elevation of suitable habitats for *R. bieti* was found to increase by approximately 97–109 m under scenario-c, scenario-d, scenario-e and scenario-f, and decrease by 8 m under scenario-b (Table 1). The permutation of importance of variables indicated that collecting and grazing were the most important factors affecting range contraction under scenario-b and scenario-c, whereas mean temperature during the driest three-month period (Mtdq) and temperature constancy (Iso) were the most important factors under scenario-a and scenario-c (Appendices 4–5).

The circuit model predicted that in the year 2050 there would continue to be high habitat connectivity, defined as the possibility for *R. bieti* to expand its range or for individuals to migrate between populations under scenario-a, followed by scenario-c and scenario-b (Fig. 3). All three scenarios predicted greater habitat connectivity among *R. bieti* groups inhabiting the Honglaxueshan and Baimaxueshan Nature Reserves, while the lowest habitat connectivity is expected to occur among the southern groups in the Jinsichang and Yunling Nature Reserves (Fig. 3). Migration analyses revealed asymmetrical gene flow in the Baimaxueshan Nature Reserve and low levels of genetic exchange in Yunling and Jinsichang (Fig. 4). Also, there were unique haplotypes (M1-M4 and M6-M11) in Yunling and Jinshichang (M29–30) and very limited gene flow between *R. bieti* groups inhabiting both the Yunling and Jinsichang Nature Reserves (Fig. 4).

4. Discussion

Among China's 25 species of nonhuman primates, 70% have a remaining wild population of < 3000 individuals. Thus, protecting China's threatened primate populations is a national priority (Estrada et al., 2017; Li et al., 2018). We found that in the case of the endangered *R. bieti* (current population size of < 3000 individuals), the collection of forest products by local villagers and the conversion of forest into pasture land for grazing cattle have resulted in severe fragmentation of natural landscapes (e.g., habitat disturbance) and these two types of disturbances are projected to represent the primary drivers of habitat reduction for this species over the next 30 years. We also found that some areas predicted by the model as suitable habitat are unsuitable for *R. bieti* because these regions are highly fragmented and have limited opportunities for migration and gene flow, resulting in a critical loss of genetic diversity.

4.1. Effects of hunting on R. bieti's distribution

The expansion of roads and infrastructure into remote areas is likely to promote human accessibility, illegal colonization, and hunting (Laurance et al., 2015; Peres and Lake, 2003). Our model includes proxies of hunting such as distance from settlements and roads, which are useful predictors of hunting pressures. Between the 1960's to the 1990's, hunting was one of the greatest threats to *R. bieti* survivorship, as local villagers hunted this species for meat, fur, and as traditional medicine. This led to a sharp decrease in its distribution and population size (Long et al., 1994). Our model suggests that the availability of suitable habitat for *R. bieti* is the lowest under scenario-b and that collecting forest products, cattle grazing, and the distance to settlements, a proxy for hunting pressure, have had an important negative effect on the species' historical distribution (Table.1, Appendix 4 and Fig. 3b). For example, in Indonesia and Africa the hunting of large bodied apes such as orangutans, bonobos, and western chimpanzee, along with the conversion of forest to planted monocultures and agricultural fields is reported to have resulted in severe population decline (Hickey et al., 2013; Kühl et al., 2017; Marshall et al., 2009; Santika et al., 2017). In contrast, in the case of *R. bieti*, hunting currently has a very limited direct effect on survivorship due to the enactment by the Chinese government in 1988 of the Wildlife Protection Act. This act listed *R. bieti* within the first class of key protected animals in China. In addition, the establishment and improvement of national nature reserves and the strict state control of firearms, has protected subpopulations of *R. bieti* residing inside these protected areas, and in some areas this has resulted in an increase in the size of the remaining local populations (Zhao et al., 2018).

4.2. Collecting-grazing and climate change contract the distribution of R. bieti

Anthropogenic activities are rapidly transforming our planet and are the primary cause of biodiversity loss (Ellis and Ramankutty, 2008; Pimm et al., 2014). Our results show the area of suitable habitat for the endangered *R. bieti* in 2050 is predicted to contract under three modeled scenarios (scenario-a, scenario-b and scenario-c, Table 1 and Fig. 2). However, controlling for anthropogenic activities, the area of suitable habitat in 2050 was predicted to increase (Table 1 and Fig. 2). Collecting and grazing are expected to have a markedly negative effect on the availability of suitable habitat for *R. bieti*, and therefore increased monitoring of protected areas by park rangers and public programs focused on conservation education are needed.

Behavioral observations indicate that *R. bieti*, which requires a large supply area (exploits a home range of 40 km^2, Grueter et al., 2008; Kirkpatrick and Grueter, 2010, and lives in groups of several hundred individuals) alters its pattern of habitat utilization in the presence of humans (Li et al., 2014) and in human modified landscapes (Clark et al., 2009; Crooks et al., 2017). For example, data collected by Li et al. (2005) on a closely related snub-nosed monkey species, the golden-snub-nosed monkey (*R. roxellana*), indicate that groups living in areas heavily disturbed by humans increased their day range by 42%–45% compared to groups living in areas of limited human disturbance. Studies of several mammalian species indicate that stimuli and disturbance resulting from the presence of humans in the forest can disrupt ranging behavior and patterns of habitat utilization (Frid and Dill, 2002; Fernández-Juricic and Schroeder, 2003; Steidl and Anthony, 2000). In areas occupied by *R. bieti*, the activities of local villagers including entering the forest to search for and collect medicinal plants (e.g. *Cordyceps sinensis*) have contributed to habitat fragmentation, affecting *R. bieti* ranging patterns and population decline (Cui et al., 2006; Grueter et al., 2009). In addition, the cutting and harvesting of conifer trees, which serve as important sleeping sites for *R. bieti* and contain the species' primary year-round food resource, lichen (*Usnea* spp., *Bryoria* spp.) also has a severe impact on *R. bieti* survivorship (Grueter et al., 2009).

In addition, populations of *R. bieti* face a set of severe anthropogenic challenges in parts of its range in which large areas of primary forest have been converted into pastures for cattle grazing (Xiao et al., 2003). The negative environmental impacts of expanding pastures and the increased reliance by local villagers on livestock, which leads to a reduction in biodiversity, changes in soil nutrient composition, and a decrease in soil fertility and soil porosity (Reiners et al., 1994), are expected to further exacerbate the effects of climate change on *R. bieti*

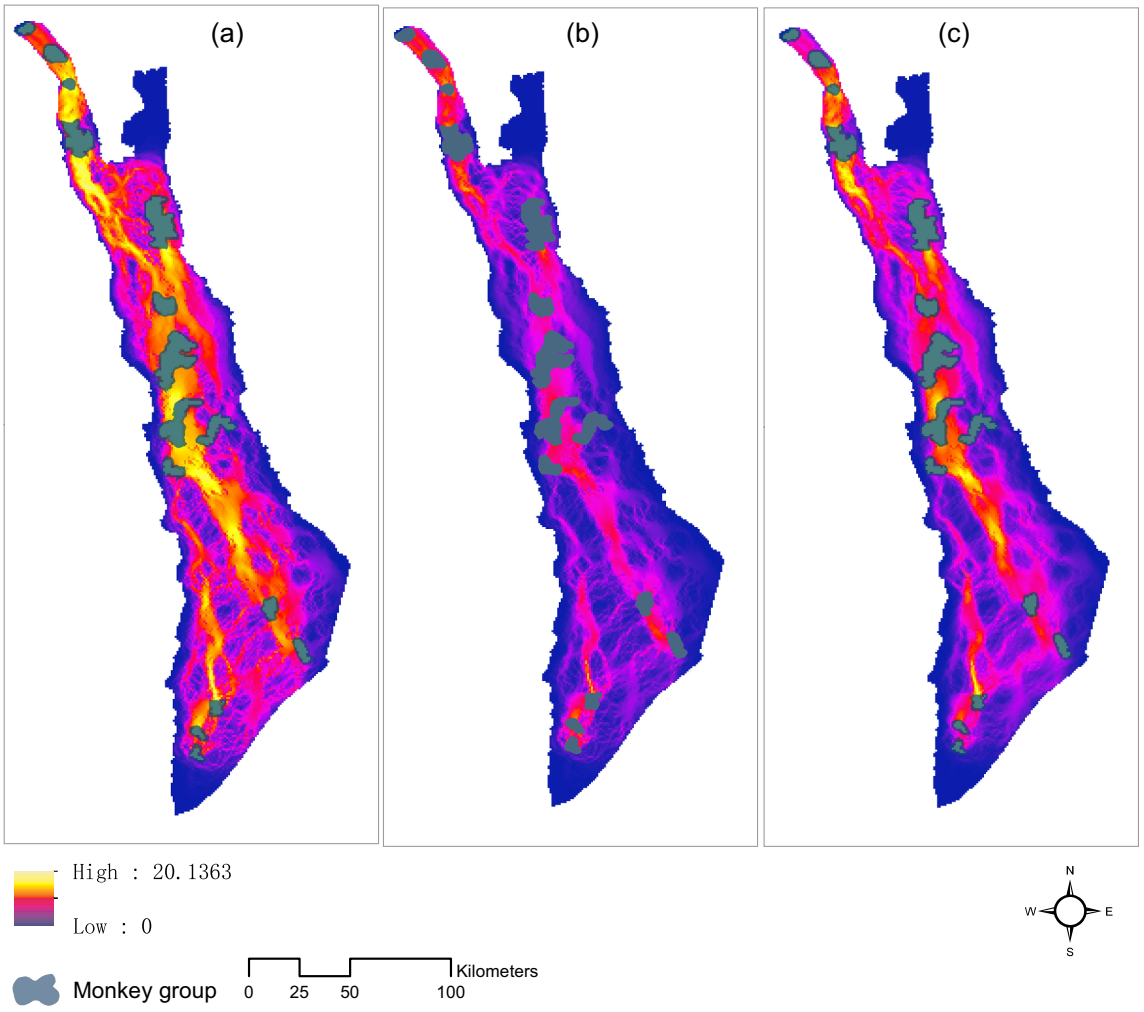

Fig. 3. Predicted habitat connectivity using the circuit model for the year 2050. (a), (b) and (c) indicate habitat connectivity under scenario-a (a), scenario-b (b) and scenario-c (c).

range contraction (Tuanmu et al., 2013), leading to a reduction in food availability, increased habitat fragmentation, and increased sub-population isolation (Li et al., 2017). The expansion of cattle grazing in China also has had a negative effect on habitat availability for the giant panda (*Ailuropoda melanoleuca*) and threatens the long-term survival of this species (Li et al., 2017). Based on our observations that *R. bieti* avoids areas of livestock, particularly cattle, and that pastures function as a barrier limiting *R. bieti* dispersal, the expansion of pastureland remains a critical factor in their long-term survivability (Grueter et al., 2010).

In addition, our model predicted that temperature (Isothermality and Mean Temperature of Driest Quarter) is an important factor affecting the distribution of *R. bieti*. Given its pattern of breeding seasonality, temperature might act as a reproductive regulator for the onset of estrus and mating in *R. bieti* (Cozzolino et al., 1992; Huang et al., 2012). In addition, environment factors only (scenario-a) and environment factors and anthropogenic activities (scenario-c, scenario-d, scenario-e, scenario-f) are predicted to result in an increase in the elevation of suitable habitat for *R. bieti* by approximately 97–109 m. However, anthropogenic activities only (scenario-b) are predicted to result in an decrease of 8 m in the altitudinal expansion of suitable habitat. Thus continued increases in global temperature are expected to impact habitat availability for *R. bieti*. Our results are consistent with a global trend in which recent temperature increases have caused several species to migrate toward the poles or regions of higher elevation (Parmesan and Yohe, 2003; Root et al., 2003). In addition, > 50% of the *R. bieti*'s diet consists of lichen and increased temperatures have a negative effect on lichen abundance (Aptroot, 2009; Grueter et al., 2009). Therefore, an increase in temperature leading to a contraction of the distribution and availability of lichen, especially at low elevations, is expected to result in the loss of previously suitable habitat for *R. bieti*.

4.3. Habitat connectivity and gene flow

Based on the circuit model, habitat connectivity was highest under scenario-a, followed by scenario-b and scenario-c, which suggested that anthropogenic activities have had a strong negative effect on habitat connectivity(Fig. 3). However, data from our surveys indicate that there exist areas within the Baimaxueshan and Honglaxueshan Nature Reserves that can be expanded via a program of habitat connectivity (Fig. 3c). Baimaxueshan and Honglaxueshan remain connected by forest corridors that serve as links between habitat patches, whereas groups of *R. bieti* at Yunling and Jinsichang are isolated and corridors for migration and gene exchange no longer exist (Fig. 3) (Li et al., 2014). This is crucial because barriers to migration continue to result in limited opportunities for individuals to move between isolated sub-populations in the Yunling and Jinsichang nature reserves (Fig. 3). In addition, National Road 214 passes through the middle of Yunling and Jinsichang, and this has resulted in a decrease in habitat connectivity among *R. bieti* populations in this region (Li et al., 2014). There remain difficulties in assessing connectivity using resistance surfaces derived from habitat models. This is due to the fact that habitat suitability may

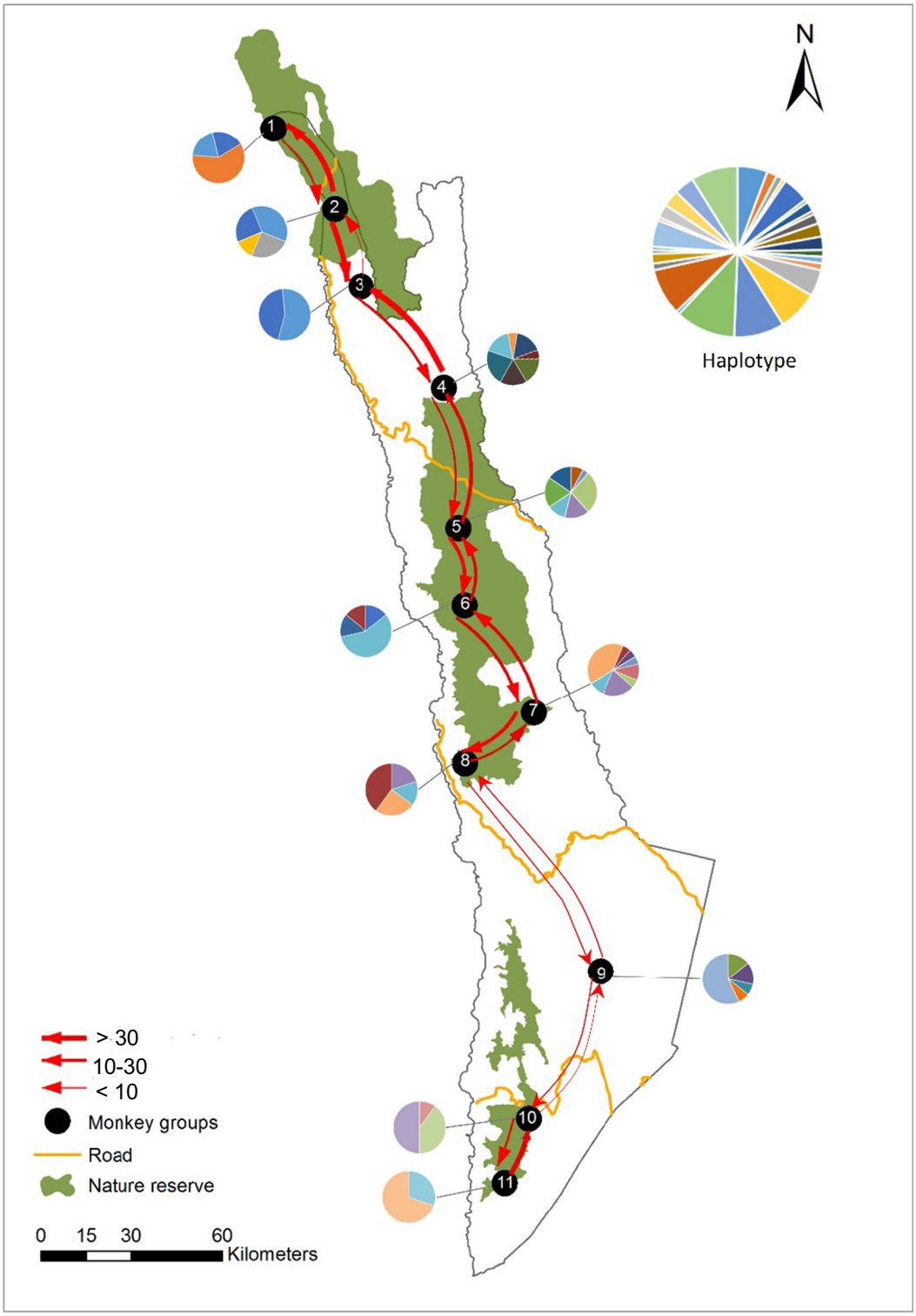

Fig. 4. Geographical distribution of haplotypes and gene flow between adjacent subpopulations of the *R. bieti*. Colors indicate the types of haplotypes. Groups 1 to 11 indicated: Zhina, Milaka, Bamei, Wuyapuya, Cikatong, Guyoulong, Xiangguqing Anyi, Jinsichang, Fuheshan, and Longma.

not adequately reflect the relationship between environment and animal movement (Elliot et al., 2014; Roever et al., 2014). Therefore, an assessment of landscape permeability for animal movement must consider landscape characteristics and species-specific movement and dispersal patterns (Ziółkowska et al., 2016). In the case of the brown bear (*Ursus arctos*), resistance surfaces derived from the habitat models were found to underestimate habitat connectivity (Ziółkowska et al., 2016).

Habitat fragmentation strongly correlates with a reduction in gene flow and population-level genetic variability across a wide range of mammalian and avian taxa (Balkenhol and Landguth, 2011; Jaquiery et al., 2011). And, although, our study focused on a single primate species, the conservation modeling approaches presented here have wide applicability to a broad range of threatened species that are affected by the conversion of natural habitat to pasture, increased hunting pressure, forest fragmentation, itinerant mining, and the effects of climate change on the availability of suitable habitat. For example,

an analogous modeling approach examining the effects of fragmentation on species-richness in subtropical forest avian communities in Brazil, Argentina, and Paraguay Hanski et al. (2013) found that species declines resulted from both local extinctions in individual habitat fragments and to nonviable metapopulations in highly fragmented landscapes (Hanski et al., 2013). Thus, we suggest that habitat connectivity can be used to predict the risk of future extirpations of small or isolated animal populations (He et al., 2010; Manel et al., 2003). In the present study, we found that there was low habitat connectivity among *R. bieti* groups in Yunling and Jinsichang (Fig. 3), and this has led to limited gene flow among groups (Fig. 4). Given the high risk of declining genetic diversity, in the absence of increased habitat connectivity via natural or human-made corridors, we fear the extirpation of the endangered *R. bieti* in Yunling and Jinsichang is inevitable.

5. Conclusion

Species distribution modeling is a widely used tool in conservation planning and management (Guisan and Thuiller, 2005). Our models indicate that unless anthropogenic activities that result in environmental degradation and fragmentation, including the collection of forest products by local human communities and the grazing of cattle, are highly controlled and regulated, the endangered populations of *R. bieti* inhabiting areas of relatively low altitude (3000–3500 m) forests in the Yunling and Jinsichang nature reserve will continue to reduce in size, become genetically isolated, and go extinct. Our results highlight the importance of including anthropogenic activities (e.g. collecting and grazing), habitat connectivity (areas of forest fragmentation, open pastures, villages and roads) and genetic diversity, when modeling the distribution of non-volant endangered species characterized by small and declining population size and limited geographical distribution. Adding the activities of the local human communities, such as collecting forest products and grazing, into environmental models, provides additional explanatory power and improves the model's performance.

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